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THE SENSORY BASIS OF COURTSHIP

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Courtship may be defined as an elaborate sexual response involving recognition, selection, and pursuit. Although these various phases of behavior may be complicated by elaboration of details and variation of execution, the "pattern" of courtship, as generally understood, is easily recognized whenever and wherever it occurs. Selection, though it involves individuals is accompanied or preceded by the recognition of characteristics both specific and sexual. These may precede or follow pursuit, according to conditions. That is to say, recognition and even selection are seldom infallible, as any one who has studied the courtship of insects knows.

For in many species courtship regularly precedes sexual union. This is notably true of diurnal, flying forms; indeed it is a form of behavior typical of "daylight" species. In those rare cases where courtship occurs among nocturnal insects (*e.g.*, the Lampyridæ) one will find that there is special provision for the stimulation of the visual senses.

Courtship is, in fact, an almost exclusively *visual* process; courting animals (not insects exclusively) depend almost entirely upon the visual impressions they receive. Why is this the case, and what relation does it have to the property of being diurnal? I believe that the explanation is contained in two conditions; the high degree of acuity of daylight vision which makes possible the recognition of patterns, and the restriction of elab-

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orate patterns to species inhabiting intense light. Correlary to these conditions is the fact that the visual senses are the only senses sufficiently discriminating to make such behavior possible.

Night vision, even in animals primarily or exclusively nocturnal, is not only generally insensitive to differences to color, but is also less sensitive than daylight vision to form and depth; this is true of both vertebrates and arthropods. Animals active both during the day and at night certainly have the resolving power of the eyes reduced in weak light. It is, in fact, impossible to separate color vision absolutely from the perception of form, since, to considerable extent, the latter condition depends upon the condition known as "simultaneous contrast." The truth of this is indicated by the familiar examples found in human color-blindness; as, for example, the difficulty experienced in locating a red apple among green foliage.

But to recognize a pattern implies the presence of a pattern to recognize, and it is also true that the formation of brilliant, strongly contrasting pigments is directly dependent upon exposure to intense illumination. Caverniculous animals are unpigmented; so too, are many insects inhabiting the trunks of trees or which are subterranean in habit; and the eggs of most species of birds nesting in hollow trees or underground burrows are white. Most nocturnal animals, though pigmented, are dull in color, and, more significantly, do not exhibit the striking color patterns characteristic of diurnal forms.

This relationship of light to pattern is especially obvious among insects. The wing-patterns of moths lack both the distinctness of line and brilliancy of color so consistently present in their diurnal relatives, the butterflies. Moths which are diurnal generally have acute vision, distinct color patterns, and exhibit some inclination to courtship, although their behavior in this respect is less intricate than that of the butterflies. Parenthetically, most butterflies are much more sensitive to the longer rays of the visible spectrum than are the nocturnal moths, and animals sensitive to the longer spectral rays appear to have a higher visual acuity than those insensitive to the red end of the spectrum.

Most of the large, silk-producing moths (*Saturnidæ*) are

strictly nocturnal. The males are attracted to the females by odor, and mating occurs without any intervening courtship. But I have found that *Callosamia promethia* not infrequently flies and mates by day, and this moth exhibits so striking a difference in the color patterns of the two sexes that the uninformed laymen often mistakes them for distinct species. I have not seen this moth exhibit courtship, although I have read somewhere that actual experiments made in transferring the wings of one sex to the other gave results indicating some visual sex recognition. But even if courtship is lacking in this species, we need not be surprised, since phyletically sex differentiation probably has preceded the development of courtship behavior to some extent; indeed it could hardly be otherwise.

Also significant is the fact that the flashing of fireflies is a visual stimulus to sexual union; but it constitutes a part of the courtship itself. It differs from diurnal courtship also in the fact that instead of depending upon a fixed pattern for recognition, the same result is achieved by a "time pattern." That is to say, each species has a flash frequency which is specific both as to the duration of the glow and the interval of darkness; recognition depends upon these alone.

As one might expect, courtship is particularly characteristic of predatory insects, even though their very nature makes the sexes potential enemies. The reason for this is obvious, since predatory forms are generally visually acute. Dragonflies, for example, refute the popular dogma that the bulk of initiative in courtship is masculine. Recently I observed with interest the mating behavior of an unidentified species of *Enallagma*. Females as well as males pursued other females; not infrequently a female insect pursued a male. Because the life of the predatory insect depends upon the *pursuit* of prey, it may be that the pursuit of a potential mate is initiated by the same impulse. Students of human psychology have often remarked that the impulses concerned with nutrition and reproduction are inextricably interwoven.

The behavior of animals other than insects supports the conclusions here set forth. For instance, birds, which have been cited as the animals exhibiting courtship in its most intricate

and highly specialized forms are predominantly diurnal and predominantly dependent upon vision. Also, most of them are predatory, for it is impossible to regard insectivorous birds as otherwise than predators in a broad sense, nor is it possible to draw a distinct line between insectivorous forms and those predatory upon other animals. Song, it is true, plays a minor role in the courtship of birds, but this also has its counterpart among such insects as cicadas and grasshoppers.

To recapitulate: courtship among animals depends directly upon diurnal habits, acute vision, and the development of patterns. Among insects this is almost exclusively the case, and it is generally true elsewhere in the animal kingdom. The exhibition of courtship does not depend upon taxonomic relationships, except such as are related to the requirements described.